Diversity and Distributions

WILEY

Diversity and Distributions

RESEARCH ARTICLE OPEN ACCESS

Pollinator Interactions of Native and Introduced Plants in Smallholder Tropical Orchards Across a Gradient of Anthropogenic Landscapes

Kanuengnit Wayo[1,2,3] | Tuanjit Sritongchuay[4,5,6] | Pattraporn Simla[7] | Suntaree Karnchananiyom[8] | Tuan Ngoc Nguyen[9,10] | Orawan Duangphakdee[11] | Mark van Kleunen[12,13]

[1]ZUKOnnect Fellow, Zukunftskolleg, University of Konstanz, Konstanz, Germany | [2]Futuristic Science Research Center, School of Science, Walailak University, Nakhon Si Thammarat, Thailand | [3]Research Center for Theoretical Simulation and Applied Research in Bioscience and Sensing, Walailak University, Nakhon Si Thammarat, Thailand | [4]Department Computational Landscape Ecology, UFZ – Helmholtz Centre for Environmental Research, Leipzig, Germany | [5]Chair of Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg, Germany | [6]Department of Environmental Science and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway | [7]Conservation Ecology Program, School of Bioresources and Technology, King Mongkut's University of Technology Thonburi, Bangkok, Thailand | [8]Department of Plant Science, Faculty of Science, Mahidol University, Bangkok, Thailand | [9]Faculty of Crop Science, College of Agriculture, Can Tho University, Can Tho, Vietnam | [10]Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, Thailand | [11]Native Honeybee and Pollinator Research Center, Ratchaburi Campus, King Mongkut's University of Technology Thonburi, Ratchaburi, Thailand | [12]Department of Biology, University of Konstanz, Konstanz, Germany | [13]Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China

Correspondence: Mark van Kleunen (mark.vankleunen@uni-konstanz.de)

Received: 22 November 2024 | **Revised:** 4 July 2025 | **Accepted:** 10 July 2025

Editor: Aibin Zhan

Funding: This work was supported by the Zukunftskolleg, Universität Konstanz (ZUKOnnect Fellowship) award to K.W. This work was mainly carried out in Zukunftskolleg at the University of Konstanz, Germany.

Keywords: agricultural area | landscape composition | land-use change | pollination network | specialisation | urbanisation

ABSTRACT

Aim: Anthropogenic habitats commonly favour introduced species. However, there is little information regarding the responses of pollinators to native and introduced plants across anthropogenic landscapes. The main goal of the study is to investigate pollinator interactions of native and introduced plants across smallholder tropical orchards in Thailand, as these plantations are essential to local food security.

Location: Smallholder tropical orchards in Thailand.

Methods: We compiled data from four recent studies on plant–pollinator networks in 65 smallholder tropical orchards across Thailand. Using network analyses, we compared species degree (i.e., the number of pollinator species visiting a plant) and specialisation (d') between native and introduced plant species, with the latter further categorised into non-naturalised, naturalised and invasive groups. Analyses were conducted using linear mixed-effects models (LMMs), treating individual plant species as the unit of analysis and incorporating orchard identity nested within study as a random effect. Additionally, we examined whether variation in surrounding anthropogenic landscapes (i.e., the proportion of agricultural and urbanised areas) and the proportional representation of introduced plant species influenced the structure of plant–pollinator networks.

Results: Overall, specialisation (d') of the native plants was significantly greater than that of the introduced plants, while pollinators exhibited no preference towards naturalised or invasive plants over non-naturalised ones. We found a decrease in species degree of native plants as well as connectance and linkage density with increasing proportion of anthropogenic areas, likely due

---

to limited floral resources and nesting availability. However, we also found an increase in network specialisation (H_2') with a higher proportion of urban area.

Main Conclusions: Understanding the impact of land-use changes with the presence of introduced plant species is important for predicting community stability of plant–pollinator interactions as well as for habitat management strategies. Surrounding natural habitat and important food plants should be preserved and promoted to maintain pollinator interactions in human-dominated areas.

1 | Introduction

Mutualistic plant–pollinator interactions are important, as most flowering plants require animals for pollination (Rodger et al. 2021), and most animal pollinators rely on flowering plants for food sources. Besides native plants, introduced plants may be key food sources for pollinators (Bartomeus et al. 2008; Graves and Shapiro 2003). Since introduced plant species frequently depend on native pollinators to successfully establish (Aizen et al. 2008; Bartomeus et al. 2008; Memmott and Waser 2002), it is essential to understand how introduced species interact with existing pollinator communities compared to native species.

Although non-native flowering plants are visited by native pollinators (Arroyo-Correa et al. 2020; Drossart et al. 2017; Williams et al. 2011), some non-native plants with more attractive and larger or more flowers can outcompete native plants for pollinators (Morales and Traveset 2009). Among the introduced plants, especially the ones that are considered invasive, can cause disruptions to mutualistic interactions between native plants and pollinators (Traveset and Richardson 2006). For example, introduced plants may compete with native ones for visitation by pollinators and might also reduce seed production through increasing heterospecific pollen transfer (Chittka and Schürkens 2001; Malecore et al. 2021). Thus, understanding the importance of pollinator interactions between native and introduced plants is key for habitat management in order to conserve potential pollinators and native plant communities.

It is well established that human land-use change has reduced natural vegetation, which provides primary floral resources such as nectar and pollen to wild pollinators, and thereby negatively influences the mutualistic association between plants and pollinators (Baude et al. 2016; Winfree et al. 2011). This may lead to pollinator declines (Potts et al. 2010). For example, the diversity of pollinators on crops has been found to decline with increasing distance to natural habitats (Carvalheiro et al. 2010; Ricketts et al. 2008). It has also been found that pollinator-dependent plants in urban settings are more pollen-limited than those in managed and natural landscapes (Bennett et al. 2020). While numerous studies have investigated the impact of land-use change on pollination networks in tropical and temperate regions (e.g., Larkin and Stanley 2023; Proesmans et al. 2024; Sritongchuay et al. 2019), few have examined how such changes influence the roles of native and introduced plants in these networks (e.g., Muñoz-Galicia et al. 2023; Zaninotto et al. 2023), particularly in Asian countries. Our study addresses this gap by focusing on how land-use changes affect pollinator interactions with native plant species and invasive, naturalised and non-naturalised introduced plant species, as well as human-food plants. We expect native plants to exhibit more specialised interactions due to co-evolution with local pollinators. In contrast, introduced species vary in their degree of integration: invasive and naturalised species are typically more embedded in networks, showing higher generalisation and interaction degrees and often occupying key topological roles such as hubs or connectors (Albrecht et al. 2014). Non-naturalised species, by comparison, receive fewer flower visitors (Razanajatovo et al. 2015) and are less integrated into networks. This research will offer new insights into how anthropogenic landscapes uniquely influence the structure of pollination networks in Southeast Asia.

This study examined how plant origin and landscape context influence pollination networks in smallholder tropical orchards. Specifically, we addressed three main objectives. First, we compared species-level pollination network metrics—namely, the number of pollinator species visiting each plant (species degree) and species-level specialisation (d')—among native, invasive, naturalised and non-naturalised introduced plant species. Second, we examined whether surrounding anthropogenic landscapes, measured as the proportions of agricultural and urbanised areas, influenced these species-level metrics between native and introduced plants. Finally, we tested how network-level metrics—connectance, linkage density and network-level specialisation (H_2')—were affected by the proportional representation of introduced plant species visited by pollinators in each orchard, the extent of anthropogenic landscapes and the interaction between these factors. We hypothesised that native plants, due to their long co-evolutionary history with local pollinators, would attract more pollinator species (higher species degree) and exhibit more specialised interactions (higher d') than introduced plants. Additionally, we predicted that higher levels of anthropogenic land use would promote more generalised interactions, particularly for introduced species, which often exhibit traits—such as abundant, large, or accessible flowers—that attract generalist pollinators commonly found in disturbed habitats.

2 | Materials and Methods

2.1 | Data Compilation

To investigate how landscape composition influences pollinator interactions of native and introduced plants in smallholder tropical orchards, we compiled data provided by previous studies on plant–pollinator networks in smallholder tropical orchards across Thailand. We selected four recent studies for our analyses, including Karnchananiyom et al. (2024), Sritongchuay et al. (2022), Simla et al. (2022) and

Wayo et al. (2020) (Table S1). These studies were conducted in different regions of Thailand and varied in the prevalence of introduced plant species (Table S2). Wayo et al. (2020) focused on how local and landscape features influence stingless bee communities and pollination networks in southern Thailand. Simla et al. (2022) examined the effects of invasive plants and land-use composition on insect pollinators in the northeast. Sritongchuay et al. (2022) investigated the impacts of landscape context on diurnal and nocturnal flower visitors—including insects and bats—across the south, central and north. Karnchananiyom et al. (2024) assessed how local and landscape factors shape bee community composition in the south. Although these studies provided data from 106 smallholder tropical orchards, 10 orchards from Wayo et al. (2020) lacked pollination network data and were excluded. The final dataset comprised 96 orchards representing a broad gradient of anthropogenic landscapes across Thailand (Figure 1).

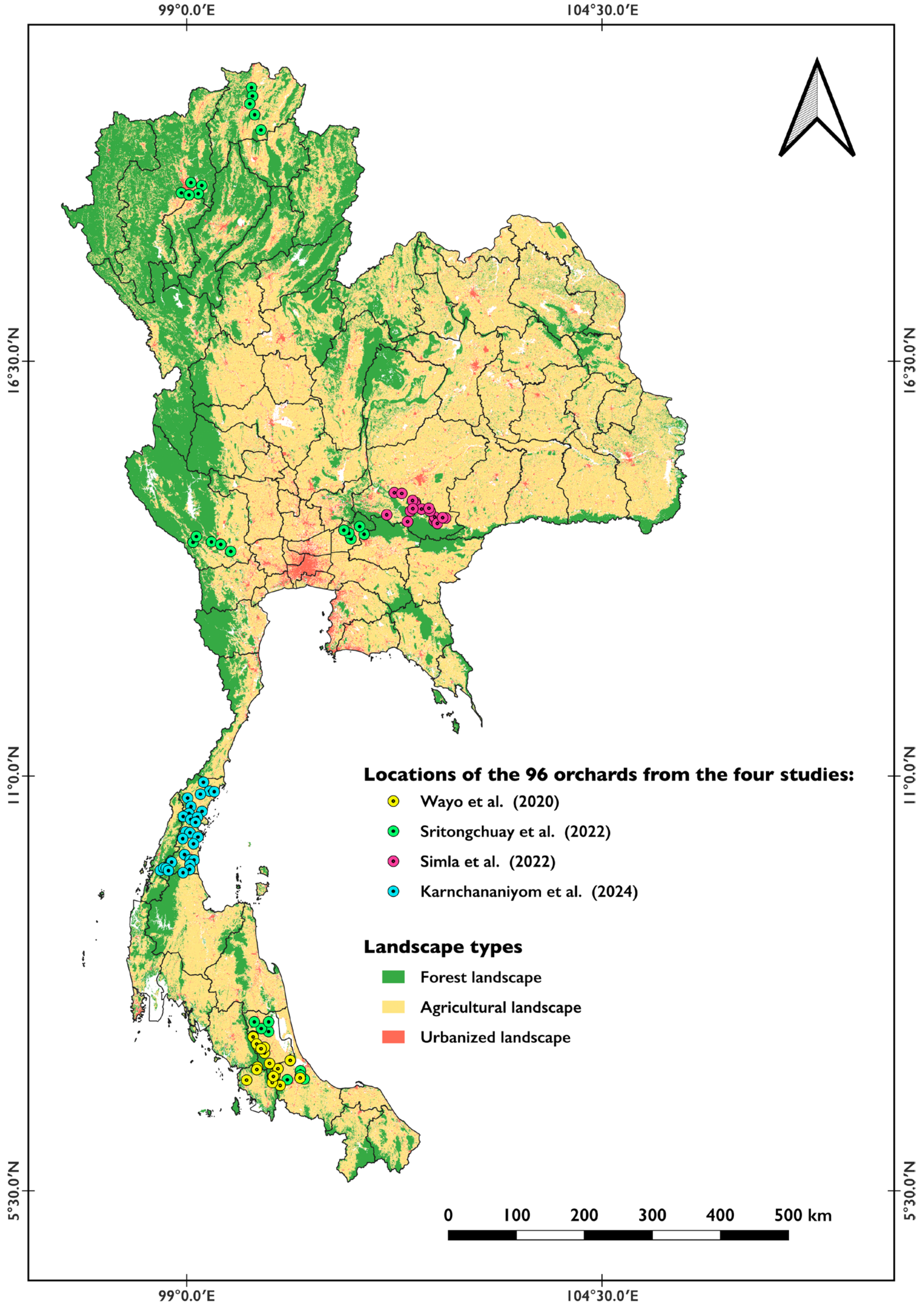

FIGURE 1 | The locations of the 96 smallholder tropical orchards that we used in our analyses covered a gradient of anthropogenic landscapes in Thailand. The data originate from Simla et al. (2022), Sritongchuay et al. (2022), Wayo et al. (2020) and Karnchananiyom et al. (2024). The map was produced using QGIS software (QGIS.org 2023).

2.2 | Plant Categories

We considered only flowering plants which were visited by pollinators and identified to the species level, according to the data provided by the four selected studies. These studies aimed to document pollinator interactions across the complete set of co-blooming plant species within each orchard. We then categorised the flowering plant species into either native or introduced species based on their native distributions provided by the Plants of the World Online website (POWO 2022). When a plant species was not indicated as being native to Thailand in these databases, we considered it to be introduced to Thailand. We further divided introduced plant species into three categories, i.e., non-naturalised, naturalised and invasive plant species, using a checklist of the naturalised plant species of Thailand obtained from the Global Naturalised Alien Flora database (van Kleunen et al. 2019) and a checklist of the invasive plant species of Thailand (Zungsontiporn et al. 2020). Naturalised plants are defined as introduced plant species that have established self-sustaining populations without direct intervention by humans (Richardson et al. 2000), whereas invasive plants are naturalised plants that have negative ecological or socio-economic impacts (CBD 2000). Although invasive species are a subset of naturalised species, we here separated them into separate categories. In other words, the naturalised species in our study are not categorically invasive. Moreover, to obtain a list of species that are most likely cultivated by humans for food production, we used the information from the World Checklist of Useful Plant Species (Diazgranados et al. 2020) to check which of the native and introduced species are known to be used as human food. Furthermore, although *Salacca magnifica* Mogea, *Ocimum* × *africanum* Lour., *Sterculia monosperma* Vent., *Musa* × *paradisiaca* L., *Glochidion wallichianum* Müll.Arg., *Citrus* × *aurantiifolia* (Christm.) Swingle were not listed as human-food plants in Diazgranados et al. (2020); they are vegetables and fruits and thus were also categorised as human food plants.

2.3 | Network Construction

We constructed plant–pollinator networks in the R program (R Core Team 2023) using the *plotweb* function (‘bipartite’ package) (Dormann et al. 2008). Although the four studies provided plant–pollinator-interaction data for 96 smallholder tropical orchards, we selected only orchards containing more than five plant species visited by pollinators (see Table S2 for details). Therefore, 65 orchards in total were included in our network analyses. To construct the pollination networks, we created for each orchard a pollinator-visitation matrix. Each matrix comprised interactions observed between plant species (columns) and pollinator species (rows). The cell values were the number of observations for each pollinator species by plant species combination. Depending on the study, this was measured as the number of pollinator visits to or the number of pollinator individuals that visited each plant species. We calculated pollination network structure at the species level, including species degree (i.e., the sum of links or the number of interacting pollinator species per plant species) and specialisation (d') of each plant species using the *specieslevel* function in the ‘bipartite’ package (Dormann 2011). The d' value is a species-level specialisation index within the network, and ranges from 0 (generalist) to 1 (perfect specialists) (Blüthgen et al. 2006). At the network level, we used the *networklevel* function (‘bipartite’ package; Dormann et al. 2009) to calculate connectance, linkage density and specialisation (H_2'). Connectance is the realised proportion of possible links in the network (i.e., sum of links divided by number of cells in the matrix) (Dormann et al. 2009), and linkage density is the quantitative diversity of interactions per species weighted by the marginal sum of interactions (Vanbergen et al. 2017). H_2' is a network-level specialisation index and ranges from 0 (no specialisation) to 1 (complete specialisation) (Blüthgen et al. 2006).

3 | Statistical Analyses

To compare differences in the species-level pollination-network metrics (1) between native and introduced plants, (2) between naturalised and non-naturalised introduced plants, (3) between naturalised and invasive plants, (4) between food plants for humans only and non-human-food plants and (5) between native human-food and introduced human-food plants, we applied LMMs implemented in the ‘lme4’ (Bates et al. 2015) and ‘lmerTest’ (Kuznetsova et al. 2017) packages. To account for variation in sampling effort and spatial clustering, we specified *Orchard_ID* nested within *Study_ID* as a random effect in all models. This hierarchical structure controlled for differences in study design, regional context and observer effort across the four studies. Individual plant species served as the unit of analysis, and plant category was included as a fixed effect. Species degree was natural-log transformed, and specialisation (d') was square-root transformed to improve normality. We assessed residual normality and homoscedasticity for all models using the *check_model* function from the ‘performance’ package (Lüdecke et al. 2021). Explanatory power was evaluated using marginal R^2 (variance explained by fixed effects) and conditional R^2 (variance explained by fixed and random effects) (Nakagawa and Schielzeth 2013), calculated with the *r.squaredGLMM* function from the ‘MuMIn’ package (Bartoń 2024). To control for false discovery rate in multiple comparisons, raw p-values were adjusted using the Benjamini–Hochberg procedure (Benjamini and Hochberg 1995) separately for each species-level metric, and statistical significance was determined based on the adjusted p-values.

To explore the impact of land-use change on the structure of pollination networks in smallholder tropical orchards, we used land-use data as reported by each original study. These landscape proportions were derived from GIS analyses performed by the original authors of each study. For studies that focused exclusively on insect pollinators (Karnchananiyom et al. 2024; Simla et al. 2022; Wayo et al. 2020), land-use data were derived within a 3-km radius. In contrast, for the study that included insect and bat pollinators (Sritongchuay et al. 2022), a 5-km radius was used to reflect the broader foraging range of bats (Table S2).

To investigate whether an increase in the proportion of anthropogenic landscapes around the orchards influenced the species-level metrics (species degree and d') for the native and introduced plant categories, we used LMMs. The proportions of agricultural and urbanised areas, which were not significantly correlated (Pearson's $r = 0.12$, $p = 0.33$), were included as fixed effects. Plant species served as the unit of analysis, and *Orchard_ID* nested within *Study_ID* was modelled as a random effect to account for the hierarchical structure of the data. To improve normality, species degree was natural-log transformed and specialisation (d') was square-root transformed.

To test the effects of proportions of surrounding agricultural area (AG), urbanised area (UR), the proportional representation of introduced plant species visited by pollinators within each orchard (INTRO), and their interactions (AG:INTRO and UR:INTRO) on the network-level metrics (connectance, linkage density, and H_2'), we used LMMs. We included *Study_ID* as a random effect in all models. Linkage density was log-transformed to improve normality.

For model selection, we started with the most complex model, which included all explanatory variables, and then stepwise removed non-significant interactions/variables. We assessed significance by comparing each model with a given explanatory variable to the same model without this variable using the *anova* function ('lme4' package) (based on likelihood-ratio tests and chi-square statistics). We plotted the corresponding linear regression line with its 95% CI using the *ggpredict* function in the 'ggeffects' package (Lüdecke 2018) and the "ggplot2" package (Wickham 2016). All statistical analyses were performed in R (R Core Team 2023).

4 | Results

4.1 | Plant–Pollinator Interactions at the Species Level

The plant–pollinator interactions data for the 96 smallholder tropical orchards in Thailand included 210 flowering plant species visited by pollinators, representing 68 families (Table S6), and among those plant species, 124 species (59.05%) are introduced species. Among those introduced plants, 72 species (58.07%), 47 species (37.90%) and 5 species (4.03%) are considered non-naturalised, naturalised and invasive, respectively. The invasive species include *Chromolaena odorata* (L.) R.M. King & H. Rob., *Cleome rutidosperma* DC., *Leucaena leucocephala* (Lam.) de Wit, *Tithonia diversifolia* (Hemsl.) A. Gray and *Sphagneticola trilobata* (L.) Pruski. Additionally, we found that 166 species (79.05%) are considered human-food plants. Of these, 64 species (38.55%) are native human-food plants, while 102 species (61.45%) are introduced human-food plants.

Our LMMs revealed distinct patterns in species-level network metrics across plant groups (Figures 2 and 3, Table S3). For native versus introduced plants, species degree did not differ significantly ($t = 2.01$, $p_{adj} = 0.184$), whereas native species showed significantly greater specialisation (d') ($t = 2.58$, $p_{adj} = 0.044$). No significant differences were detected between non-naturalised and naturalised plants in either species degree ($t = 0.84$, $p_{adj} = 0.447$) or specialisation ($t = 0.57$, $p_{adj} = 0.569$). Similarly, species degree ($t = 1.59$, $p_{adj} = 0.184$) and specialisation ($t = 1.07$, $p_{adj} = 0.320$) did not differ significantly between naturalised and invasive plants. For human-food versus non-human-food plants, neither species degree ($t = 0.23$, $p_{adj} = 0.820$) nor specialisation ($t = 1.19$, $p_{adj} = 0.293$) differed significantly. However, when comparing native human-food versus introduced human-food plants, only specialisation was significantly higher in native species ($t = 2.66$, $p_{adj} = 0.044$), while species degree showed no significant difference ($t = 2.21$, $p_{adj} = 0.184$).

In addition, our results show that plant–pollinator interactions at the species level were influenced by landscape composition (Figures 4 and 5, Table S4). The proportion of agricultural areas had a significantly negative effect on the species degree of native plants (LMM: $\chi^2 = 5.315$, df = 1, $p = 0.021$), but not on that of introduced plants ($\chi^2 = 1.009$, df = 1, $p > 0.05$). The proportion of urbanised areas did not significantly affect species degree for either native ($\chi^2 = 2.010$, df = 1, $p > 0.05$) or introduced ($\chi^2 = 0.441$, df = 1, $p > 0.05$) plants. For the specialisation (d'), neither the proportion of agricultural nor urbanised areas significantly influenced the metric for native (agricultural: $\chi^2 = 0.001$; urban: $\chi^2 = 3.246$; both $p > 0.05$) or introduced plants (agricultural: $\chi^2 = 1.874$; urban: $\chi^2 = 1.021$; both $p > 0.05$).

4.2 | Plant–Pollinator Interactions at the Network Level

Our LMMs showed the effects of the proportion of surrounding agricultural and urbanised areas, the proportional representation of introduced plant species visited by pollinators in each orchard, and their interactions on network-level metrics (Figure 6, Table S5). Overall, none of the interaction terms had significant effects. In addition, the proportional representation of introduced plant species did not significantly influence connectance ($\chi^2 = 0.220$, df = 1, $p > 0.05$; Figure 6G), linkage density ($\chi^2 = 2.689$, df = 1, $p > 0.05$; Figure 6H), or network-level specialisation (H_2'; $\chi^2 = 0.208$, df = 1, $p > 0.05$; Figure 6I).

For the effects of anthropogenic landscapes, our results revealed that connectance was negatively affected by the proportion of urbanised areas ($\chi^2 = 8.976$, df = 1, $p = 0.003$; Figure 6D) but was not significantly affected by agricultural areas ($\chi^2 = 1.159$, df = 1, $p > 0.05$; Figure 6A). In contrast, linkage density was negatively affected by the proportion of agricultural areas ($\chi^2 = 4.326$, df = 1, $p = 0.038$; Figure 6B) but was not significantly affected by urbanised areas ($\chi^2 = 0.455$, df = 1, $p > 0.05$; Figure 6E). In addition, H_2' increased significantly with the proportion of urbanised areas ($\chi^2 = 7.676$, df = 1, $p = 0.006$; Figure 6F) but was not significantly affected by agricultural areas ($\chi^2 = 0.466$, df = 1, $p > 0.05$; Figure 6C).

5 | Discussion

Our study analysed pollinator interactions among native plant species and invasive, naturalised and non-naturalised introduced plant species and the effects of landscape composition on the structure of pollination networks at the species and network levels in smallholder tropical orchards. At the species level, there are two important results: (1) the specialisation (d') was significantly greater for native plants than for introduced plants, and (2) the proportion of surrounding agricultural areas

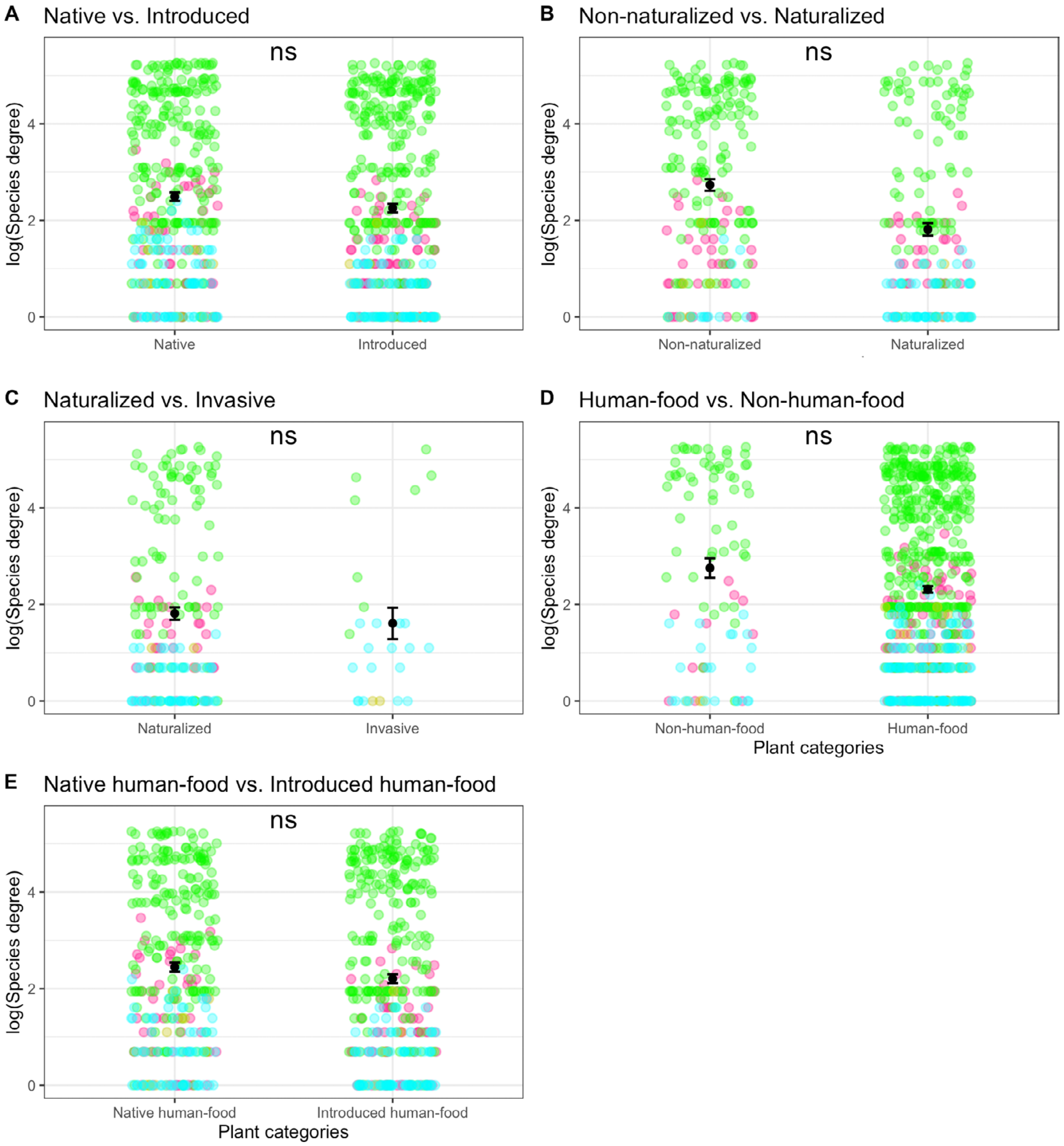

FIGURE 2 | Mean (± standard error) of log-transformed species degree across plant categories (A–E) in tropical orchards. Each point represents a single plant species, with colours denoting the study of origin: Simla et al. (2022) (pink), Sritongchuay et al. (2022) (green), Wayo et al. (2020) (yellow) and Karnchananiyom et al. (2024) (blue). Significance: ns = non-significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

had a significantly negative effect on the species degree of native plants. At the network level, connectance and linkage density were negatively affected by the proportions of urbanised areas and agricultural areas, respectively, whilst network specialisation (H_2') was positively affected by the proportion of urbanised areas.

5.1 | Plant–Pollinator Interactions at the Species Level

Overall, native plant species had significantly more specialised interactions than introduced plant species in our study. This pattern also held when considering only human-food plants: native human-food plants exhibited more specialised interactions than their introduced counterparts. This likely reflects the longer evolutionary history that native plants share with local pollinators, which has facilitated the emergence of more specialised mutualisms. Such specialisation is commonly attributed to co-evolutionary processes, whereby floral traits become fine-tuned to the behavioural preferences and morphological traits of particular pollinator groups (Fenster et al. 2004; Johnson and Steiner 2000). Our finding is consistent with a recent study showing that native plants had more specialised plant–bee visitation networks than non-native plants, while non-native plants associated with generalist bees (Seitz et al. 2020). Although we found that pollinators overall did not exhibit stronger preferences towards naturalised or invasive plants relative to non-naturalised introduced plants in Thailand's smallholder tropical orchards, our findings overall indicate that introduced flowering plants can integrate into existing pollination networks. This is consistent with previous research showing that introduced species often form interactions with generalist pollinators and become functionally embedded within native plant–pollinator communities (e.g., Bartomeus et al. 2008; Aizen et al. 2008). Approximately 60%

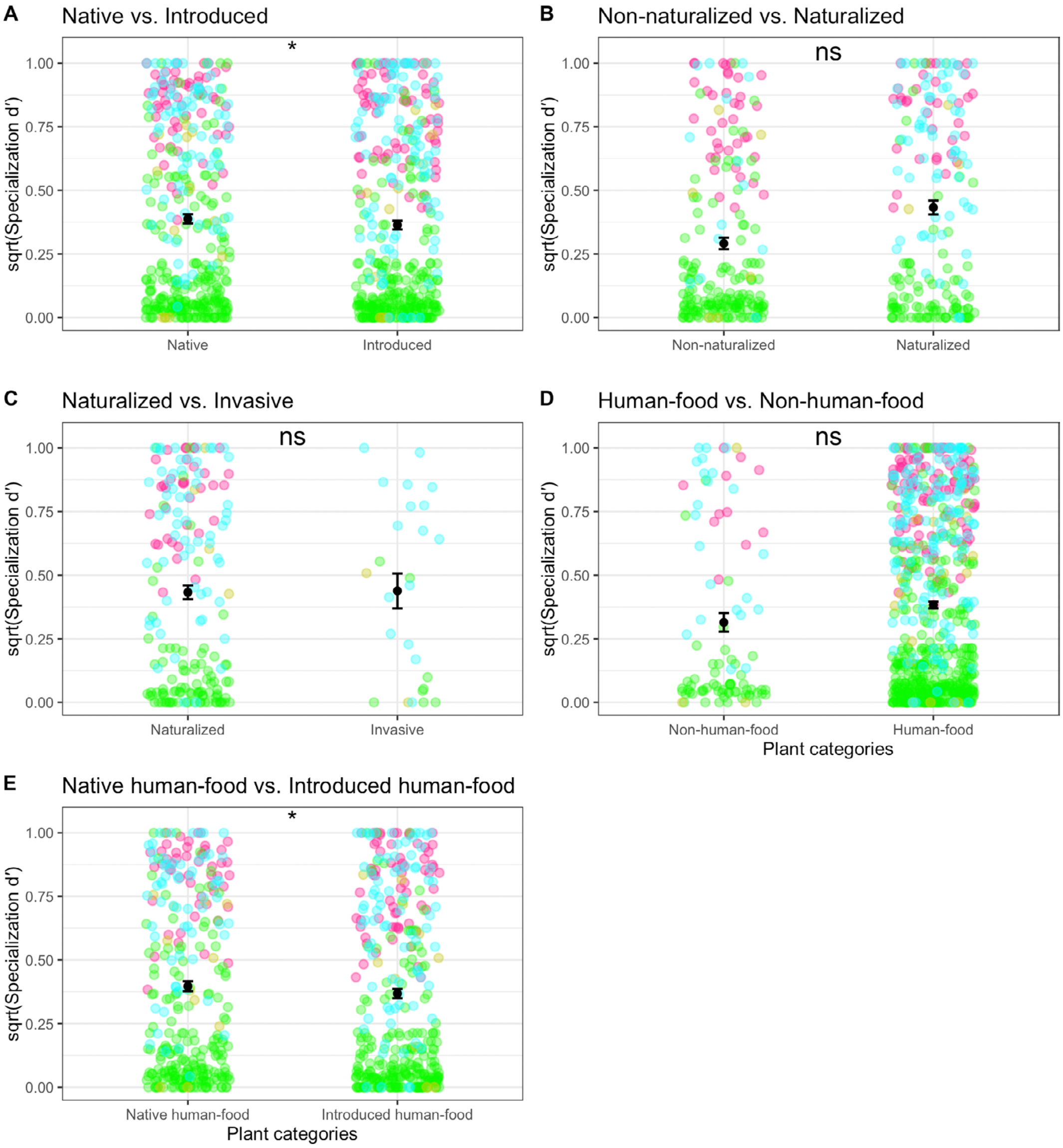

FIGURE 3 | Mean (± standard error) of square root-transformed specialisation (d') across plant categories (A–E) in tropical orchards. Each point represents a single plant species, with colours denoting the study of origin: Simla et al. (2022) (pink), Sritongchuay et al. (2022) (green), Wayo et al. (2020) (yellow) and Karnchananiyom et al. (2024) (blue). Significance: ns = non-significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

of all flowering plant species visited by pollinators in the study were introduced plants, which may serve as important food sources for pollinators alongside native plants (Bartomeus et al. 2008; Graves and Shapiro 2003), especially during periods when native plants are not in bloom.

As expected, our findings highlight that in orchards with higher proportions of surrounding agricultural areas, native plant species attracted fewer pollinators. To assess whether a lack of forest-dwelling pollinators drove this pattern, we included the proportion of surrounding forest as a fixed effect in additional models. Although forest cover was negatively correlated with agricultural ($r = -0.43$, $p < 0.001$) and urban ($r = -0.33$, $p = 0.007$) land uses, it did not significantly affect species degree ($p = 0.175$) or specialisation (d') ($p = 0.064$) of native plants. These results suggest that the decline in pollinator interactions is more strongly associated with increasing anthropogenic land use than with forest loss alone. Moreover, pollinator richness and abundance tend to be low in predominantly agricultural landscapes due to limited floral resources and nesting availability, particularly for solitary bees and stingless bees (Karnchananiyom et al. 2024; Wayo et al. 2020), resulting in low visitation by pollinators in native plant communities. Although we lacked data on the presence of mass-flowering crops, previous research suggests that such crops can dilute pollinator abundance in adjacent habitats (Holzschuh et al. 2016). Future studies incorporating remote sensing or detailed crop mapping would help clarify which land-use types are driving these effects. Additionally, agrochemical use may further reduce pollinator visitation to native flora (Bloom et al. 2021).

In contrast to our expectations, the proportion of surrounding urbanised area did not significantly influence the number of pollinator species (species degree) or specialisation (d') for either native or introduced plants. Although urbanisation

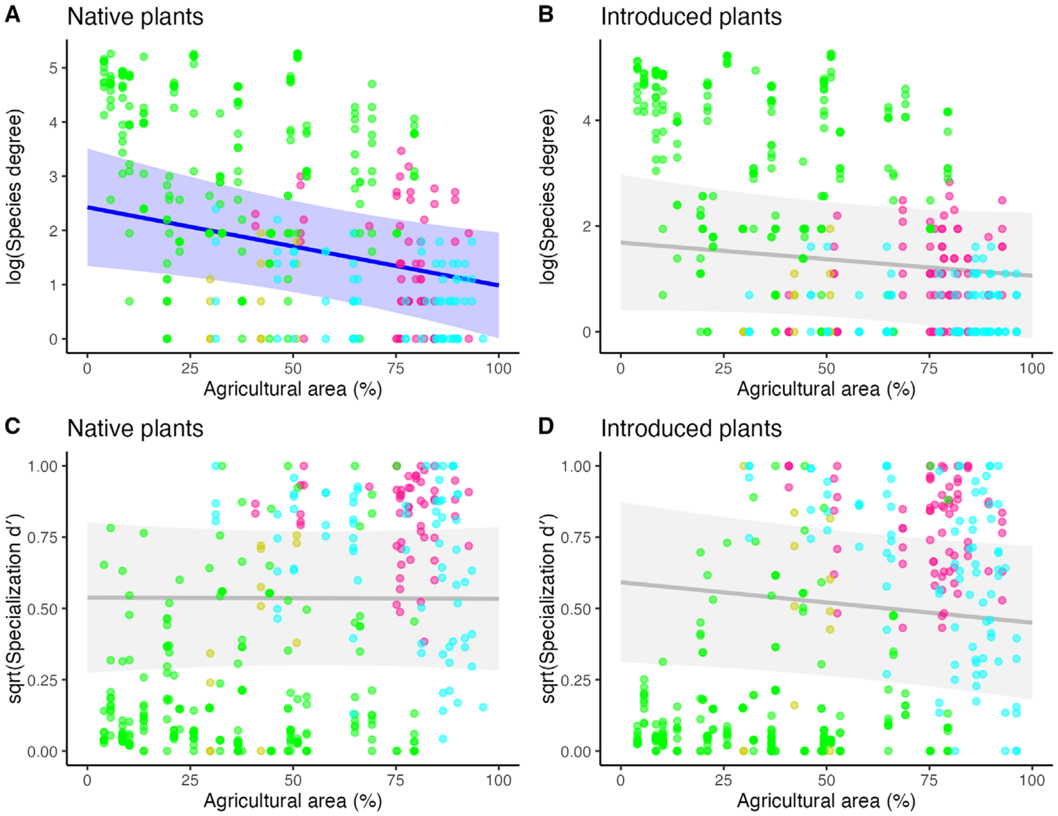

FIGURE 4 | Effects of the proportion of surrounding agricultural area on species degree and specialisation (d') for native (A, C) and introduced (B, D) plant categories across 65 smallholder tropical orchards in Thailand. Linear mixed-effects model (LMM) regressions are shown with 95% confidence intervals. A significant relationship is indicated by a blue line, while nonsignificant relationships are shown in grey. Each point represents a single plant species, with colours denoting the study of origin: Simla et al. (2022) (pink), Sritongchuay et al. (2022) (green), Wayo et al. (2020) (yellow) and Karnchananiyom et al. (2024) (blue).

is generally associated with reduced pollinator richness and abundance (Millard et al. 2021; Liang et al. 2023), the relatively low urban land cover in our study (0%–28%) may have limited our ability to detect such effects. Future research incorporating a broader urbanisation gradient is needed to clarify how increasing urban development influences plant–pollinator interactions.

5.2 | Landscape Effects on Plant–Pollinator Interactions at the Network Level

Our findings demonstrate how the landscape composition influenced the plant–pollinator network-level metrics. Specifically, the connectance of the pollination networks decreased with increasing urban cover, likely reflecting a reduction in the proportion of realised interactions relative to all possible plant–pollinator interactions. This pattern may result from increased specialisation in urban areas, where highly specialised species are present but contribute relatively few interactions (Blüthgen et al. 2006). The decline in connectance implies a reduction in the complexity and robustness of the network. Network specialisation (H_2') increased with greater proportions of surrounding urbanised areas in this study. While urbanisation is typically associated with generalist pollinators, recent studies suggest that behavioural changes can increase interaction exclusivity. For example, Theodorou et al. (2017) observed that urban pollinators visited a narrower subset of plant species, resulting in higher network specialisation. Suni et al. (2022) proposed that in fragmented urban habitats, pollinators may specialise more due to energetic constraints and the cost of moving between isolated patches. Once in a suitable site, they may focus foraging on fewer plant species to maximise efficiency. Our findings are consistent with this possibility, and future studies should further explore how urban landscape structure shapes pollinator foraging behaviour and network dynamics.

While connectance and specialisation of the networks were not affected by the proportion of agricultural area surrounding the orchard, linkage density declined as agricultural land increased. This pattern likely reflects differences in the underlying pollinator species pools across land-use types: species richness, abundance and community composition of pollinators often differ significantly between landscapes, with natural or semi-natural habitats supporting higher diversity and abundance compared to urban or intensively managed agricultural areas (Winfree et al. 2009). In our study, the decline in linkage density may result from reduced pollinator abundance and richness in agricultural landscapes—driven by limited floral resources and nesting opportunities (Karnchananiyom et al. 2024; Wayo et al. 2020)—which lowers the average number of unique interactions per species. As a result, the networks become less

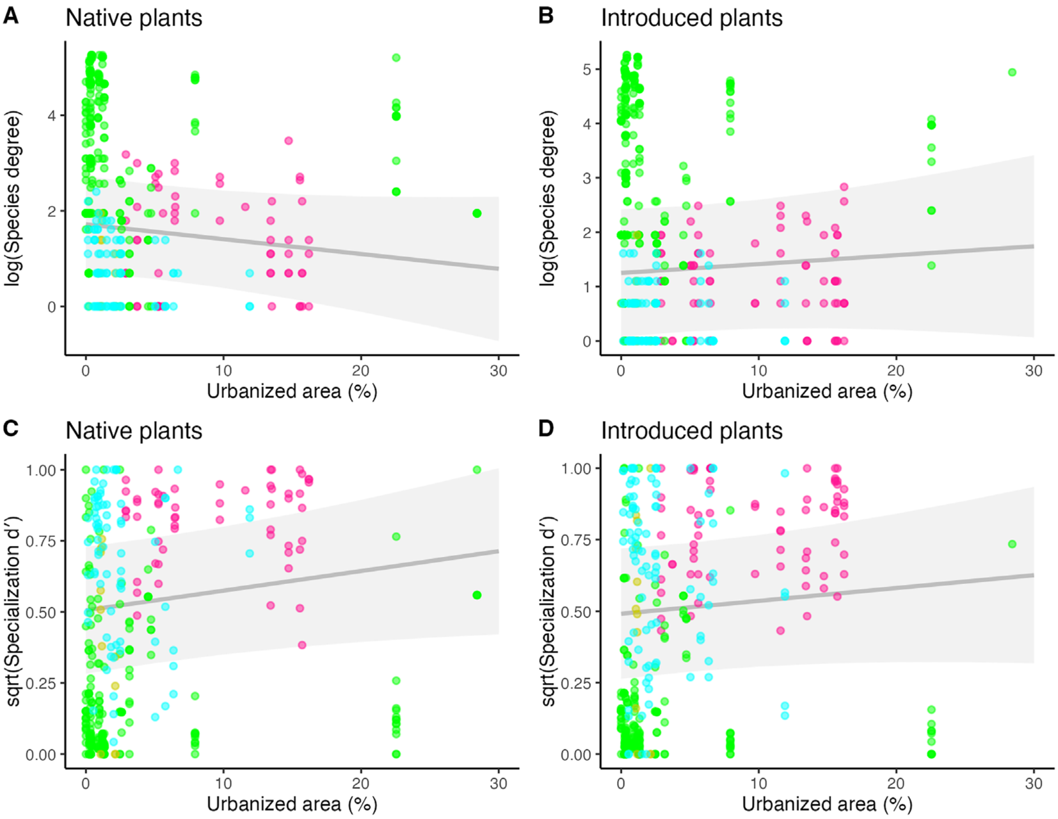

FIGURE 5 | Effects of the proportion of surrounding urbanised area on species degree and specialisation (*d′*) for native (A, C) and introduced (B, D) plant categories across 65 smallholder tropical orchards in Thailand. Linear mixed-effects model (LMM) regressions are shown with 95% confidence intervals. Nonsignificant relationships are indicated by grey lines. Each point represents a single plant species, with colours denoting the study of origin: Simla et al. (2022) (pink), Sritongchuay et al. (2022) (green), Wayo et al. (2020) (yellow) and Karnchananiyom et al. (2024) (blue).

complex, potentially reducing their robustness and the reliability of pollination services. In contrast, connectance—the proportion of realised to possible interactions—remained relatively stable, likely reflecting the persistence of generalist interactions even under diminished community diversity.

6 | Implications for Landscape Management

Our study provides important information on food plants (both native and introduced flowering plant species) for pollinators in orchards surrounded by different proportions of agricultural land and urbanised areas. Our findings highlight the integration of introduced flowering plants into pollination networks across agricultural and urban landscapes. Although we found no significant differences among introduced plant categories or effects of their proportional representation, their widespread presence suggests they may influence long-term network dynamics. Invasive species with abundant floral displays may draw pollinators away from native plants, potentially disrupting reproduction and altering pollinator foraging behaviour (Morales and Traveset 2009; Vanbergen et al. 2018). Future research on trait compatibility and temporal overlap with pollinators could help predict which species may become ecologically dominant and destabilise mutualistic networks (Fournier et al. 2019). Additionally, given the global increase in naturalised plant species (van Kleunen et al. 2015), long-term monitoring is essential to assess how invasive species may influence pollination dynamics over time.

Our findings also inform landscape management and pollinator conservation, particularly habitat design for smallholder tropical orchards. It is essential to understand the food preferences of pollinator communities in order to effectively restore optimal pollinator habitat. To support sustainable pollination services, we recommend farmers conserve surrounding natural habitats and promote native plant abundance within human-dominated landscapes—not only because native plants support a higher diversity of pollinators but also because increasing anthropogenic land use may simplify pollination networks, potentially reducing the resilience and functional integrity of these ecosystems. Our findings highlight that native plants support a higher diversity of pollinators and play an important role in maintaining specialised plant–pollinator interactions, which are particularly vulnerable to anthropogenic pressures. Therefore, conservation efforts should prioritise restoring and maintaining native plant communities, especially within agricultural and urban landscapes. Emphasising native flora is essential for preserving the complexity of mutualistic networks and ensuring the long-term stability of pollination services. Understanding the causes and consequences of landscape variation with the presence of introduced plant species is critical for predicting community stability of plant–pollinator interactions as well as for the application of conservation

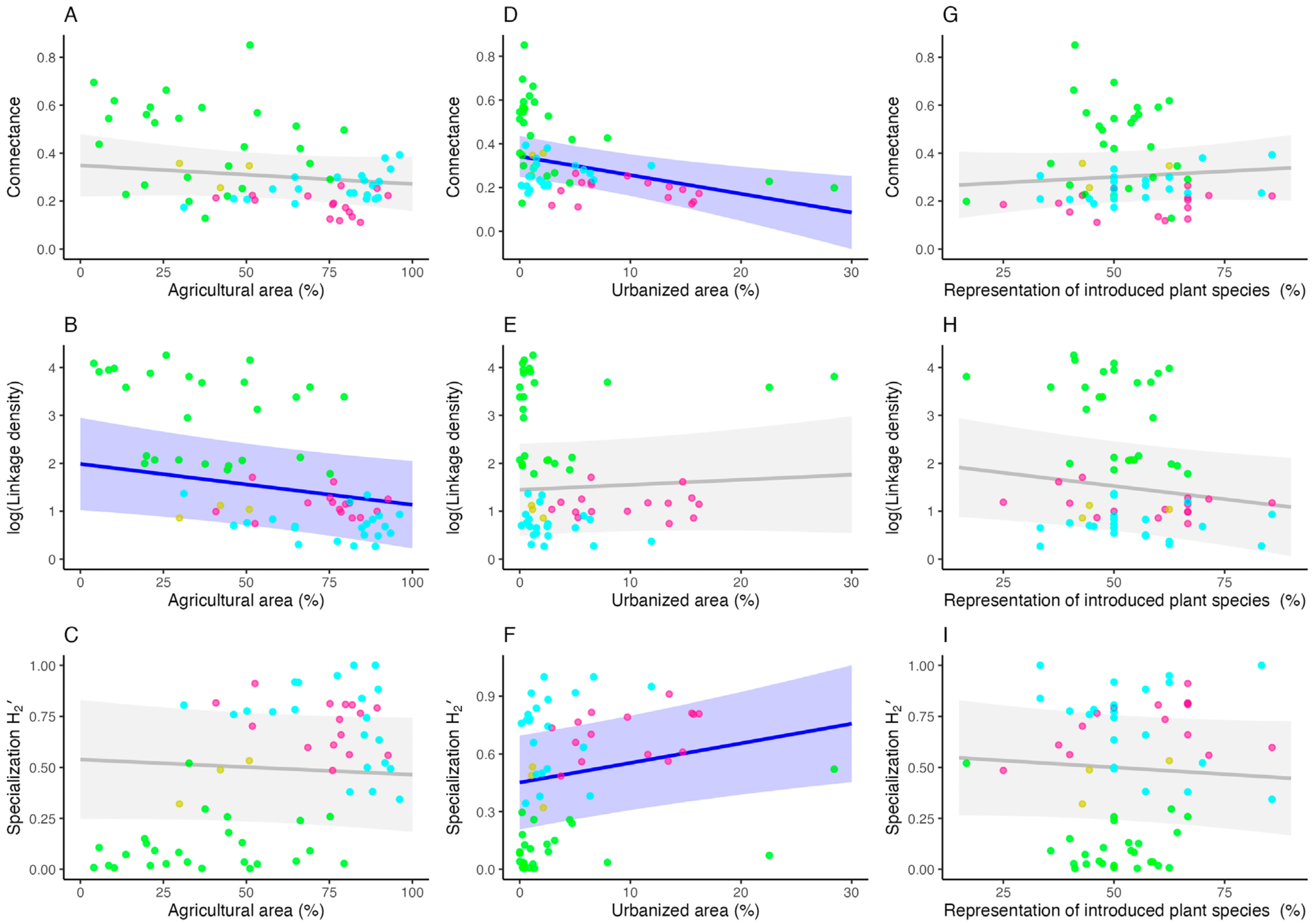

FIGURE 6 | Effects of the proportion of agricultural land (A–C), urbanised land (D–F) and the proportional representation of introduced plant species visited by pollinators (G–I) on network-level metrics across 65 smallholder tropical orchards in Thailand. All regressions are plotted with corresponding 95% confidence intervals. Significant relationships are indicated by blue lines, while nonsignificant relationships are shown in grey. Each point represents a single plant species, with colours denoting the study of origin: Simla et al. (2022) (pink), Sritongchuay et al. (2022) (green), Wayo et al. (2020) (yellow) and Karnchananiyom et al. (2024) (blue).

and landscape management strategies. Sustainable practices such as growing important native plant species, reducing pesticide use, and preserving or planting pollinator-friendly vegetation at farms' corridors can all contribute to the mitigation of the impacts of agriculture and urbanisation on pollinators.

Author Contributions

M.K., K.W., T.S. and O.D. conceived the ideas and designed the methodology; K.W., T.N.N., T.S., P.S. and S.K. prepared and compiled the data; K.W. analysed the data; K.W. and M.K. led the writing of the manuscript; all authors revised the manuscript.

Acknowledgements

The first author appreciates the support from the ZUKOnnect fellowship at the Zukunftskolleg, University of Konstanz, Germany, and the Post-doctoral Fellowship 2022 at the Native Honeybee and Pollinator Research Center, Ratchaburi Campus, King Mongkut's University of Technology Thonburi, Thailand, during data compilation and analysis. We would like to thank Eva Knop (University of Zurich) for her valuable suggestions in pollination network analyses.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in our final analyses and additional supporting information are available in Tables S1–S6.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70057.

References

Aizen, M. A., C. L. Morales, and J. M. Morales. 2008. "Invasive Mutualists Erode Native Pollination Webs." *PLoS Biology* 6, no. 2: e31. https://doi.org/10.1371/journal.pbio.0060031.

Albrecht, M., B. Padro'n, I. Bartomeus, and A. Traveset. 2014. "Consequences of Plant Invasions on Compartmentalization and Species' Roles in Plant–Pollinator Networks." *Proceedings of the Royal Society B: Biological Sciences* 281: 20140773. https://doi.org/10.1098/rspb.2014.0773.

Arroyo-Correa, B., L. A. Burkle, and C. Emer. 2020. “Alien Plants and Flower Visitors Disrupt the Seasonal Dynamics of Mutualistic Networks.” *Journal of Ecology* 108, no. 4: 1475–1486. https://doi.org/10.1111/1365-2745.13332.

Bartomeus, I., M. Vilà, and L. Santamaría. 2008. “Contrasting Effects of Invasive Plants in Plant-Pollinator Networks.” *Oecologia* 155, no. 4: 761–770. https://doi.org/10.1007/s00442-007-0946-1.

Bartoń, K. 2024. “MuMIn: Multi-Model Inference. R Package Version 1.48.4.” https://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. “Fitting Linear Mixed-Effects Models Using lme4.” *Journal of Statistical Software* 67, no. 1: 1–48.

Baude, M., W. E. Kunin, N. D. Boatman, et al. 2016. “Historical Nectar Assessment Reveals the Fall and Rise of Floral Resources in Britain.” *Nature* 530, no. 7588: 85–88. https://doi.org/10.1038/nature16532.

Benjamini, Y., and Y. Hochberg. 1995. “Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing.” *Journal of the Royal Statistical Society: Series B: Methodological* 57: 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x.

Bennett, J. M., J. A. Steets, J. H. Burns, et al. 2020. “Land Use and Pollinator Dependency Drives Global Patterns of Pollen Limitation in the Anthropocene.” *Nature Communications* 11, no. 1: 3999. https://doi.org/10.1038/s41467-020-17751-y.

Bloom, E. H., T. J. Wood, K. L. J. Hung, et al. 2021. “Synergism Between Local- and Landscape-Level Pesticides Reduces Wild Bee Floral Visitation in Pollinator-Dependent Crops.” *Journal of Applied Ecology* 58, no. 6: 1187–1198. https://doi.org/10.1111/1365-2664.13871.

Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. “Measuring Specialization in Species Interaction Networks.” *BMC Ecology* 6, no. 9: 1–12. https://doi.org/10.1186/1472-6785-6-9.

Carvalheiro, L. G., C. L. Seymour, R. Veldtman, and S. W. Nicolson. 2010. “Pollination Services Decline With Distance From Natural Habitat Even in Biodiversity-Rich Areas.” *Journal of Applied Ecology* 47, no. 4: 810–820. https://doi.org/10.1111/j.1365-2664.2010.01829.x.

CBD. 2000. “Decision V/8. Alien Species That Threaten Ecosystems, Habitats or Species.” In *UNEP/CBD/cop/5/8*. Secretariat of the Convention on Biological Diversity.

Chittka, L., and S. Schürkens. 2001. “Successful Invasion of a Floral Market.” *Nature* 411: 653.

Diazgranados, M., B. Allkin, N. Black, et al. 2020. *World Checklist of Useful Plant Species. Produced by the Royal Botanic Gardens, Kew*. Knowledge Network for Biocomplexity. https://doi.org/10.5063/F1CV4G34.

Dormann, C. F. 2011. “How to Be a Specialist? Quantifying Specialisation in Pollination Networks.” *Network Biology* 1: 1–20.

Dormann, C. F., J. Fründ, N. Blüthgen, and B. Gruber. 2009. “Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks.” *Open Ecology Journal* 2: 7–24.

Dormann, C. F., B. Gruber, and J. Fründ. 2008. “Introducing the Bipartite Package: Analysing Ecological Networks.” *R News* 8, no. 2: 8–11.

Drossart, M., D. Michez, and M. Vanderplanck. 2017. “Invasive Plants as Potential Food Resource for Native Pollinators: A Case Study With Two Invasive Species and a Generalist Bumble Bee.” *Scientific Reports* 7, no. 1: 16242. https://doi.org/10.1038/s41598-017-16054-5.

Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. “Pollination Syndromes and Floral Specialization.” *Annual Review of Ecology, Evolution, and Systematics* 35, no. 1: 375–403. https://doi.org/10.1146/annurev.ecolsys.34.011802.132347.

Fournier, A., C. Penone, M. G. Pennino, and F. Courchamp. 2019. “Predicting Future Invaders and Future Invasions.” *Proceedings of the National Academy of Sciences of the United States of America* 116, no. 16: 7905–7910. https://doi.org/10.1073/pnas.1803456116.

Graves, S. D., and A. M. Shapiro. 2003. “Exotics as Host Plants of the California Butterfly Fauna.” *Biological Conservation* 110, no. 3: 413–433. https://doi.org/10.1016/S0006-3207(02)00233-1.

Holzschuh, A., M. Dainese, J. P. González-Varo, et al. 2016. “Mass-Flowering Crops Dilute Pollinator Abundance in Agricultural Landscapes Across Europe.” *Ecology Letters* 19, no. 10: 1228–1236. https://doi.org/10.1111/ele.12657.

Johnson, S. D., and K. E. Steiner. 2000. “Generalization Versus Specialization in Plant Pollination Systems.” *Trends in Ecology & Evolution* 15, no. 4: 140–143. https://doi.org/10.1016/S0169-5347(99)01811-X.

Karnchananiyom, S., K. Wayo, T. Sritongchuay, N. Warrit, K. Attasopa, and S. Bumrungsri. 2024. “Local and Landscape Context Affects Bee Communities in Mixed Fruit Orchards in Southern Thailand.” *Agricultural and Forest Entomology* 26, no. 1: 70–80. https://doi.org/10.1111/afe.12597.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. “lmerTest Package: Tests in Linear Mixed Effects Models.” *Journal of Statistical Software* 82, no. 13: 1–26.

Larkin, M., and D. A. Stanley. 2023. “Impacts of Local and Landscape Grassland Management on the Structure of Plant-Pollinator Networks.” *Basic and Applied Ecology* 70: 50–59. https://doi.org/10.1016/j.baae.2023.04.003.

Liang, H., Y. D. He, P. Theodorou, and C. F. Yang. 2023. “The Effects of Urbanization on Pollinators and Pollination: A Meta-Analysis.” *Ecology Letters* 26, no. 9: 1629–1642. https://doi.org/10.1111/ele.14277.

Lüdecke, D. 2018. “Ggeffects: Tidy Data Frames of Marginal Effects From Regression Models.” *Journal of Open Source Software* 3, no. 26: 772. https://doi.org/10.21105/joss.00772.

Lüdecke, D., M. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. “Performance: An R Package for Assessment, Comparison and Testing of Statistical Models.” *Journal of Open Source Software* 6, no. 60: 3139. https://doi.org/10.21105/joss.03139.

Malecore, E. M., S. Berthelot, M. van Kleunen, and M. Razanajatovo. 2021. “Reciprocal Heterospecific Pollen Interference Among Alien and Native Species.” *Perspectives in Plant Ecology, Evolution and Systematics* 50: 125610. https://doi.org/10.1016/j.ppees.2021.125610.

Memmott, J., and N. M. Waser. 2002. “Integration of Alien Plants Into a Native Flower-Pollinator Visitation Web.” *Proceedings of the Royal Society B: Biological Sciences* 269, no. 1508: 2395–2399. https://doi.org/10.1098/rspb.2002.2174.

Millard, J., C. L. Outhwaite, R. Kinnersley, et al. 2021. “Global Effects of Land-Use Intensity on Local Pollinator Biodiversity.” *Nature Communications* 12, no. 1: 2902. https://doi.org/10.1038/s41467-021-23228-3.

Morales, C. L., and A. Traveset. 2009. “A Meta-Analysis of Impacts of Alien vs. Native Plants on Pollinator Visitation and Reproductive Success of Co-Flowering Native Plants.” *Ecology Letters* 12, no. 7: 716–728. https://doi.org/10.1111/j.1461-0248.2009.01319.x.

Muñoz-Galicia, D., C. Lara, C. Castillo-Guevara, M. Cuautle, and C. Rodríguez-Flores. 2023. “Impacts of Land Use Change on Native Plant-Butterfly Interaction Networks From Central Mexico.” *PeerJ* 11: e16205. https://doi.org/10.7717/PEERJ.16205.

Nakagawa, S., and H. Schielzeth. 2013. “A General and Simple Method for Obtaining R^2 From Generalized Linear Mixed-Effects Models.” *Methods in Ecology and Evolution* 4: 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. “Global Pollinator Declines: Trends, Impacts and

Drivers." *Trends in Ecology and Evolution* 25, no. 6: 345–353. https://doi.org/10.1016/j.tree.2010.01.007.

POWO. 2022. *Plants of the World Online*. Facilitated by the Royal Botanic Gardens, Kew. https://powo.science.kew.org/.

Proesmans, W., E. Felten, E. Laurent, et al. 2024. "Urbanisation and Agricultural Intensification Modulate Plant–Pollinator Network Structure and Robustness." *Functional Ecology* 38, no. 3: 628–641. https://doi.org/10.1111/1365-2435.14503.

QGIS.org. 2023. *QGIS Geographic Information System*. QGIS Association.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Razanajatovo, M., C. Föhr, M. Fischer, D. Prati, and M. van Kleunen. 2015. "Non-Naturalized Alien Plants Receive Fewer Flower Visits Than Naturalized and Native Plants in a Swiss Botanical Garden." *Biological Conservation* 182: 109–116. https://doi.org/10.1016/j.biocon.2014.11.043.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, D. F. Panetta, and C. J. West. 2000. "Naturalization and Invasion of Alien Plants: Concepts and Definitions." *Diversity and Distributions* 6, no. 2: 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x.

Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, et al. 2008. "Landscape Effects on Crop Pollination Services: Are There General Patterns?" *Ecology Letters* 11, no. 5: 499–515. https://doi.org/10.1111/j.1461-0248.2008.01157.x.

Rodger, J. G., J. M. Bennett, M. Razanajatovo, et al. 2021. "Widespread Vulnerability of Flowering Plant Seed Production to Pollinator Declines." *Science Advances* 7: eabd3524. https://doi.org/10.1126/sciadv.abd3524.

Seitz, N., D. vanEngelsdorp, and S. D. Leonhardt. 2020. "Are Native and Non-Native Pollinator Friendly Plants Equally Valuable for Native Wild Bee Communities?" *Ecology and Evolution* 10, no. 23: 12838–12850. https://doi.org/10.1002/ece3.6826.

Simla, P., T. Chaianunporn, W. Sankamethawee, A. C. Hughes, and T. Sritongchuay. 2022. "Effect of Landscape Composition and Invasive Plants on Pollination Networks of Smallholder Orchards in Northeastern Thailand." *Plants* 11: 1–19. https://doi.org/10.3390/plants11151976.

Sritongchuay, T., B. Dalsgaard, K. Wayo, et al. 2022. "Landscape-Level Effects on Pollination Networks and Fruit-Set of Crops in Tropical Small-Holder Agroecosystems." *Agriculture, Ecosystems & Environment* 339: 108112. https://doi.org/10.1016/j.agee.2022.108112.

Sritongchuay, T., A. C. Hughes, J. Memmott, and S. Bumrungsri. 2019. "Forest Proximity and Lowland Mosaic Increase Robustness of Tropical Pollination Networks in Mixed Fruit Orchards." *Landscape and Urban Planning* 192: 103646. https://doi.org/10.1016/j.landurbplan.2019.103646.

Suni, S., E. Hall, E. Bahu, and H. Hayes. 2022. "Urbanization Increases Floral Specialization of Pollinators." *Ecology and Evolution* 12, no. 3: e8619. https://doi.org/10.1002/ece3.8619.

Theodorou, P., K. Albig, R. Radzevičiūtė, et al. 2017. "The Structure of Flower Visitor Networks in Relation to Pollination Across an Agricultural to Urban Gradient." *Functional Ecology* 31, no. 4: 838–847. https://doi.org/10.1111/1365-2435.12803.

Traveset, A., and D. M. Richardson. 2006. "Biological Invasions as Disruptors of Plant Reproductive Mutualisms." *Trends in Ecology & Evolution* 21, no. 4: 208–216. https://doi.org/10.1016/j.tree.2006.01.006.

van Kleunen, M., W. Dawson, F. Essl, et al. 2015. "Global Exchange and Accumulation of Non-Native Plants." *Nature* 525: 100–103. https://doi.org/10.1038/nature14910.

van Kleunen, M., P. Pyšek, W. Dawson, et al. 2019. "The Global Naturalized Alien Flora (GloNAF) Database." *Ecology* 100, no. 1: e02542. https://doi.org/10.1002/ecy.2542.

Vanbergen, A. J., A. Espíndola, and M. A. Aizen. 2018. "Risks to Pollinators and Pollination From Invasive Alien Species." *Nature Ecology and Evolution* 2, no. 1: 16–25. https://doi.org/10.1038/s41559-017-0412-3.

Vanbergen, A. J., B. A. Woodcock, M. S. Heard, and D. S. Chapman. 2017. "Network Size, Structure and Mutualism Dependence Affect the Propensity for Plant–Pollinator Extinction Cascades." *Functional Ecology* 31, no. 6: 1285–1293. https://doi.org/10.1111/1365-2435.12823.

Wayo, K., T. Sritongchuay, B. Chuttong, K. Attasopa, and S. Bumrungsri. 2020. "Local and Landscape Compositions Influence Stingless Bee Communities and Pollination Networks in Tropical Mixed Fruit Orchards, Thailand." *Diversity* 12, no. 482: 1–18. https://doi.org/10.3390/d12120482.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag.

Williams, N. M., D. Cariveau, R. Winfree, and C. Kremen. 2011. "Bees in Disturbed Habitats Use, but Do Not Prefer, Alien Plants." *Basic and Applied Ecology* 12, no. 4: 332–341. https://doi.org/10.1016/j.baae.2010.11.008.

Winfree, R., R. Aguilar, D. P. Vázquez, G. LeBuhn, and M. A. Aizen. 2009. "A Meta-Analysis of Bees' Responses to Anthropogenic Disturbance." *Ecology* 90: 2068–2076. https://doi.org/10.1890/08-1245.1.

Winfree, R., I. Bartomeus, and D. P. Cariveau. 2011. "Native Pollinators in Anthropogenic Habitats." *Annual Review of Ecology, Evolution, and Systematics* 42: 1–22. https://doi.org/10.1146/annurev-ecolsys-102710-145042.

Zaninotto, V., E. Thebault, and I. Dajoz. 2023. "Native and Exotic Plants Play Different Roles in Urban Pollination Networks Across Seasons." *Oecologia* 201, no. 2: 525–536. https://doi.org/10.1007/s00442-023-05324-x.

Zungsontiporn, S., P. Watcharasin, A. Promma, L. J. Wong, and S. Pagad. 2020. *Global Register of Introduced and Invasive Species – Thailand*. Version 1.4. Invasive Species Specialist Group ISSG. https://cloud.gbif.org/griis/resource?r=griis-thailand&v=1.4.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.